

Northward Invasion and Range Expansion of the Invasive Fern *Thelypteris dentata* (Forssk.) St. John into the Urban Matrix of Three Prefectures in Kinki District, Japan

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ABSTRACT.—This study investigated the current distribution of an invasive tropical fern, *Thelypteris dentata*, and its habitat type in three Japanese prefectures (Osaka, Kyoto, and Shiga) in the Kinki District. The results showed that *T. dentata* has expanded its distribution into highly urbanized areas in Osaka Prefecture and has reached southern Kyoto Prefecture and central Shiga Prefecture. The distribution of *T. dentata* populations thus seems to have expanded northward based on comparisons with the distribution that was determined in the 1980s. Because the fern's habitat types were mainly the side walls or bottoms of drainage channels, crevices in stone walls and roadsides, the urban matrix has not served as a barrier to the expansion of the range of *T. dentata*; on the contrary, it may be serving as a type of heat island corridor that is facilitating the spread of this species.

KEY WORDS.—*Thelypteris dentata*, range expansion, urban heat island, global warming, greenhouse weed

The downy maiden fern (*Thelypteris dentata* (Forssk.) St. John) is considered to be an alien fern that invaded Japan from tropical or subtropical countries (Yamazumi, 1988; Hotta, 2001). In the Honshu area, the first occurrence of *T. dentata* was documented in 1951 in southern Wakayama Prefecture of Kinki District (Yamazumi, 1988). Although the fern was initially treated as a rare species (Yamazumi, 1988), by the 1970s it had been reported in several additional places, mainly in southern coastal areas of Honshu such as southern Wakayama and Mie prefectures (Manago, 1986). The Japanese distribution of *T. dentata* was described along with that of native ferns and fern allies by Kurata and Nakaike (1983). According to their survey, in the Kinki District, the fern was found at 25 locations in Wakayama Prefecture, four in Mie Prefecture, and one in Hyogo Prefecture. The ages of voucher specimens used to create this distribution map dated mainly from the 1960s to the

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beginning of the 1980s. Detailed reports of the distribution of *T. dentata* were not found in the research literature after 1983, apart from a distribution map for Wakayama Prefecture by Manago (1986). Nakajima (1998), however, predicted that the distribution of *T. dentata* might have expanded since 1983 as a result of global warming.

We investigated potential changes in the distribution of *Thelypteris dentata* since the release of its distribution map in 1983. Because we were unable to investigate changes in the national distribution of *T. dentata*, we focused on its trends in 3 prefectures (Osaka, southern Kyoto, and Shiga prefectures) in the Kinki District of western Japan. These study areas were selected because the urban heat island effect (which can facilitate the survival and growth of invasive tropical species) is remarkable in Osaka and Kyoto cities (Ohashi and Kida, 2002). The term “urban heat island” is generally used for a city or industrial site having consistently higher temperatures than the surrounding rural areas because of the greater retention of heat by buildings, concrete, and asphalt. These cities and their outskirts are thus considered to be important areas in which the relationship between increasing temperature and the expanding distribution of plant species can be investigated.

MATERIALS AND METHODS

Field investigations were carried out by one or two investigators at each site from July 2004 to October 2006. The study focused on a 500-m radius around railway stations. The main reason for selecting railway stations as the center of each study site was that it has been reported that the primary habitats of the fern are human-made habitats such as walls (Manago, 1986; Reis *et al.*, 2006) and that these habitats are common features around railway stations. In total, we surveyed 79 railway stations in central Shiga Prefecture, southern Kyoto Prefecture, and Osaka Prefecture; these included 11 stations between Yamashina and Omi-Maiko on the Kosei Line of the Japanese Railways (J. R.), 35 stations between Nagahama and Osaka on the Hokuriku Line or Tokaido Line of the J. R., 18 stations on the Osaka Loop Line of the J. R., and 15 stations between Nanba and Misaki Koen on the Nankai Honsen Line of the Nankai Railways. Downy maiden fern was not found in the additional investigations conducted around Fukui and Tsuruga Stations (which are to the north of Shiga Prefecture) in July 2005 and August 2006.

In order to investigate each site at an equivalent intensity, the maximum investigation time was set at 2 h per site. The number of individuals at each site was classified into two categories (1–10 and 10–100 individuals). The microhabitat type for each fern was classified into several categories: crevices in stone walls, side walls or the bottom of drainage channels, alleys between buildings, roadside habitats, or in planters. The populations identified by the autumn of 2005 were investigated in the following spring in order to determine whether each individual had survived the winter. The meteorological data for our study areas were collected from nearby meteorological stations by using the Japan Meteorological Agency website (Japan Meteorological Agency, 2006).

In order to investigate the increase in temperature at each site, the temperatures were compared between the two study periods (1970–1982 and 1983–2005). Two-tailed t-tests were performed for statistical analysis, with significance set at $P < 0.05$.

RESULTS

The meteorological data for our study areas are shown in Table 1. All temperatures were higher after 1983 than before; most temperatures were significantly higher, with the exception of those at Torahime and Otsu (Table 1). This was particularly true for the highly urbanized cities of Osaka and Kyoto, and for Hikone City in central Shiga Prefecture.

Individuals of the downy maiden fern were discovered at 34 of the 79 sites (43.0%; Fig. 1; Table 2). The number of individuals in each population category recorded for each site is shown in Table 2; the total count was more than 250 individuals. The main habitats of the newly discovered populations were hard-surfaced human-made habitats such as side walls or the bottom of drainage channels or stone walls. The frequency of occurrence was higher in southern Osaka Prefecture than in the other areas. The northernmost population was discovered in Hikone City, in central Shiga Prefecture. The size of this population and of individual ferns were small, but the population was discovered in the winter of 2004, and had survived for at least two years until the spring of 2006. The distance of this population from the population in Wakayama Prefecture reported by Kurata and Nakaike (1983) and Manago (1986) was approximately 100 km, and the distance from southern Hyogo Prefecture, which was the northernmost location of the fern in Kinki District in the distribution map of Kurata and Nakaike (1983), was approximately 60 km. If we assume that the fern's distribution expanded northward for a total distance of at least 60 km during a period of about 20 years, the expansion distance averages approximately 3 km per year.

DISCUSSION

Distribution of Thelypteris dentata in Japan.—We recorded 34 new populations of *Thelypteris dentata* in three prefectures of Japan's Kinki District. *Thelypteris dentata* was recorded previously in local flora lists and publications (Nakaike, 1996; Kohata, 1997; Hiratsuka City Museum, 2001; Hotta, 2001; Mitsuta, 2002; Matsui *et al.*, 2003; Murakami *et al.*, 2003, 2004; Kita-Kawachi Nature Club, 2004), and some of these reports were in Kinki District (Mitsuta, 2002; Matsui *et al.*, 2003; Murakami *et al.*, 2003, 2004; Kita-Kawachi Nature Club, 2004). Downy maiden fern was also recorded from 2000 to 2004 in forests in Osaka and Kyoto Prefectures, including fragmented forests, wildlife habitat, and reclaimed forest in urban or suburban areas (Matsui *et al.*, 2003; Murakami *et al.*, 2003, 2004). In an investigation of the fern's distribution by the Kita-Kawachi Nature Club (2004), some populations of *T. dentata* were found from central to northern Osaka Prefecture. Mitsuta

TABLE 1. Temperature data at eight meteorological stations in and near the study area. (The data were obtained from the Japan Meteorological Agency website, 2006.) The locations of each station are shown in Figure 1. The statistical significance was determined by comparing the temperatures during the two study periods (1970 to 1982 and 1983 to 2005).

	Average annual temperature (°C)			Average minimum temperature (°C)			Average maximum temperature (°C)		
	1970–1982	1983–2005	Significance of difference	1970–1982	1983–2005	Significance of difference	1970–1982	1983–2005	Significance of difference
Torahime (a)	13.2	13.9	n.s.	−6.3	−5.6	n.s.	33.7	34.8	n.s.
Hikone (b)	14.0	14.7	**	−4.8	−3.7	*	34.3	35.1	*
Otsu (c)	14.8	14.9	n.s.	−3.6	−3.4	n.s.	34.7	35.2	n.s.
Kyoto (d)	15.3	15.9	**	−4.2	−3.2	*	36.4	37.0	**
Osaka (e)	16.1	16.9	**	−2.5	−1.6	*	35.9	36.7	**
Sakai (f)	15.3	15.8	n.s.	−3.9	−3.2	n.s.	34.5	36.4	**
Kumatori (g)	14.9	15.6	*	−2.6	−2.1	n.s.	33.1	34.0	*
Wakayama (h)	16.0	16.7	**	−2.6	−1.7	**	35.3	35.7	n.s.

Differences between periods were determined using a two-tailed *t*-test: n.s., not significant; *, *p* < 0.05; **, *p* < 0.01

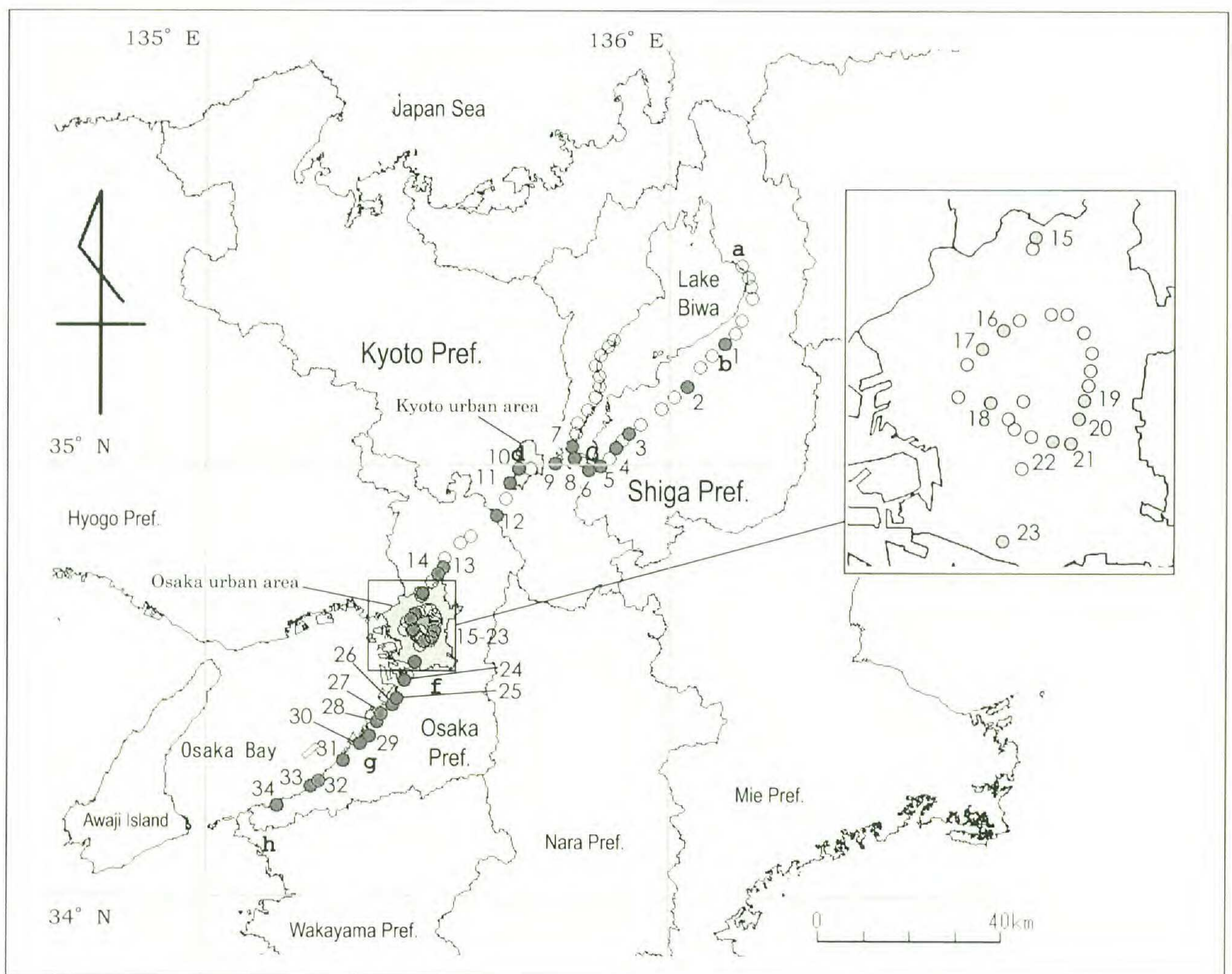


FIG. 1. Locations (the gray circles with numbers from 1 to 34) of newly discovered populations of *Thelypteris dentata* in Osaka, Kyoto, and Shiga prefectures of Japan's Kinki District. The open circles represent the study sites in which *T. dentata* was not discovered. Letters *a* through *h* represent the meteorological stations in Table 1.

(2002) also recorded *T. dentata* in a list of ferns and fern allies in Kyoto Prefecture, but did not report the locations of collected specimens or their distribution. The fern was not reported in Shiga Prefecture before the present investigation. Outside Kinki District, new populations have recently been reported from Funabashi City (Nakaike, 1996), which lies 500 km east of Osaka; in Isehara City (Hiratsuka City Museum, 2001), which lies 350 km east of Osaka; in Anjoh City (Hotta, 2001), which lies 150 km east of Osaka; and in Okayama City (Kohata, 1997), which lies 140 km west of Osaka. Because areas east or west of our study area were not investigated, it is unknown whether the fern's distribution is continuous from eastern Shiga Prefecture to Kanto Prefecture or from western Osaka Prefecture to the southern part of Chugoku Prefecture.

Some researchers noted that *T. dentata* is a species that invades new habitats by escaping from greenhouses and other artificial habitats (Uemura, 2000; Yamazumi, 1988), but it is unknown whether *T. dentata* followed this pattern in Japan. However, it is likely that many of the individuals we observed

originated in this manner because *T. dentata* is a greenhouse weed that has been reported from around the world (Wagner and Smith, 1993; Possley, 2004), and it has been observed in domestic greenhouses or accompanying potted plants in Japan (Yamazumi, 1988). We also found *T. dentata* in a greenhouse in Kyoto City in January 2006. Therefore, the probability of the fern's dispersal via greenhouses in each region seems to be high.

The current results do not clarify whether the Shiga and Kyoto populations genetically resemble the Osaka and Wakayama populations. *Thelypteris dentata* must have spread from greenhouses or potted plants purchased at floriculture stores in each area, but it is not clear whether northern individuals migrated from the southern Kinki District. However, the most important issue from the perspective of population genetics is not the dispersal routes of this species, but rather the fact that it has dispersed approximately 100 km from the Wakayama population, which was the primary location colonized by this species in the early 1980s (Fig. 2). The population identified in Moriyama City, in central Shiga Prefecture, included more than 20 full-grown individuals, thus it will not be difficult for this population to survive in the future.

The distribution of tropical species can usually be explained by the minimum winter temperature or by a cold index. The mean lowest temperature in Hikone City, which contained the northernmost population in our survey, was -3.7°C from 1983 to 2005 (Table 1). Although more detailed study is required to understand the ecology of *T. dentata*, this value provides a good preliminary indication of the threshold temperature for growth and survival of *T. dentata*.

Because of the limited area covered by our research, the populations that we discovered cannot be used to predict the northern limit of populations of this species in Kinki District. More information must be acquired in the future to confirm this limit. However, the climatic conditions in central Shiga Prefecture may be close to the northern distribution limit of the fern because the frequency of occurrence (25% of survey sites) is remarkably lower there than that in southern Osaka Prefecture (91.6% of survey sites).

Habitats of Thelypteris dentata.—During our investigation, a large population of *Thelypteris dentata* was discovered in the urban areas of Kinki District. Some individuals were also identified in central Osaka City, which is highly urban. The occurrence ratio was lower in central Osaka City (37.5%) than in the northern and southern Osaka areas (50% and 91.6%, respectively). This may have resulted from the lack of crevices at the edges of roads and the fact that fern may not be found in highly developed areas. However, some individuals were nonetheless observed in locations with large expanses of broken pavements and in walls with deep crevices, from where it was difficult to remove the fern's rhizome.

Most of the recorded microhabitat types were similar to those in previous reports (Manago, 1986; Hotta, 2001; Matsui *et al.*, 2003; Reis *et al.*, 2006): the side walls of drain channels, crevices in stone walls, roadsides, and alleys between buildings. Some individuals were discovered in pots or planters along with potted plants such as *Aloe* or *Cymbidium*. These ferns may have

TABLE 2. Locations of newly discovered populations of *Thelypteris dentata* and the associated number of individuals in each habitat type in Osaka, Kyoto and the Shiga prefectures of Kinki District, Japan. The open circles represent the *T. dentata* populations that survived from winter 2005 to spring 2006.

		Number of sites at which <i>T. dentata</i> were recorded/ Number of sites surveyed	<i>T. dentata</i> populations that survived from winter 2005 to spring 2006	Number of individuals in each microhabitat type				
Name	Location			(Crevices of) stone walls	Sidewalls or bottom of drainage channels	Inner planted pots	Roadside	Alleys between buildings
<i>Shiga Prefecture</i>		8 / 32 (25.0%)						
1	Kawase	N35°13' E136°13'	○	-	-	-	1-10	-
2	Aduchi	N35°08' E136°08'	○	1-10	1-10	-	-	-
3	Moriyama	N35°03' E135°59'	○	-	10-100	-	-	-
4	Kusatsu	N35°01' E135°57'	○	1-10	10-100	-	-	-
5	Seta	N34°59' E135°55'		10-100	-	-	-	-
6	Ishiyama	N34°58' E135°53'		-	10-100	-	-	-
7	Nishi-Otsu	N35°01' E135°51'		1-10	-	-	-	-
8	Otsu	N35°00' E135°51'	○	1-10	-	-	1-10	-
<i>Keihanshin area</i> (southern Kyoto Pref. and northern Osaka Pref.)		6 / 12 (50.0%)						
9	Yamashina	N34°59' E135°49'	○	-	-	-	1-10	-
10	Nishi Oji	N34°58' E135°43'	○	1-10	1-10	-	-	-
11	Mukoh-machi	N34°57' E135°42'	○	-	1-10	-	-	-
12	Yamazaki	N34°53' E135°40'	○	-	-	1-10	-	-
13	Senrioka	N34°47' E135°33'		-	-	1-10	-	-
14	Kishibe	N34°46' E135°32'		-	-	-	-	1-10

TABLE 2. Continued.

	Name	Location	Number of sites at which <i>T. dentata</i> were recorded/ Number of sites surveyed	<i>T. dentata</i> populations that survived from winter 2005 to spring 2006	Number of individuals in each microhabitat type				
					(Crevices of stone walls)	Sidewalls or bottom of drainage channels	Inner planted pots	Roadside	Alleys between buildings
Osaka City (central Osaka Prefecture)			9 / 23 (39.1%)						
15	Higashiyodogawa	N34°40′ E135°30′			-	-	-	1–10	-
16	Fukushima	N34°41′ E135°29′		○	10–100	-	-	-	1–10
17	Noda	N34°41′ E135°28′		○	-	-	1–10	1–10	1–10
18	Taisho	N34°39′ E135°29′		○	-	10–100	1–10	-	1–10
19	Tsuruhashi	N34°40′ E135°31′			-	-	1–10	10–100	1–10
20	Momodani	N34°39′ E135°31′			-	-	-	1–10	-
21	Terada-cho	N34°38′ E135°31′			-	-	1–10	1–10	-
22	Tennohji	N34°38′ E135°30′			-	-	-	-	1–10
23	Suminoe	N34°36′ E135°29′			-	-	-	-	10–100
Southern Osaka Prefecture			11 / 12 (91.6%)						
24	Minato	N34°34′ E135°27′			-	-	-	1–10	10–100
25	Hagoromo	N34°32′ E135°26′			-	10–100	-	10–100	-
26	Takaishi	N34°31′ E135°25′			-	10–100	-	10–100	-
27	Izumiotstu	N34°30′ E135°24′			-	10–100	-	10–100	-
28	Tadaoka	N34°29′ E135°23′			-	10–100	-	-	-
29	Kishiwada	N34°27′ E135°22′		○	10–100	10–100	-	-	-
30	Kaiduka	N34°26′ E135°21′			-	1–10	-	-	-
31	Izumisano	N34°24′ E135°19′			-	1–10	-	1–10	-
32	Tarui	N34°22′ E135°15′			1–10	10–100	-	-	-
33	Ozaki	N34°21′ E135°14′			1–10	1–10	-	-	-
34	Misaki-koen	N34°19′ E135°09′		○	1–10	-	-	-	-
Total			34		11	16	6	13	8

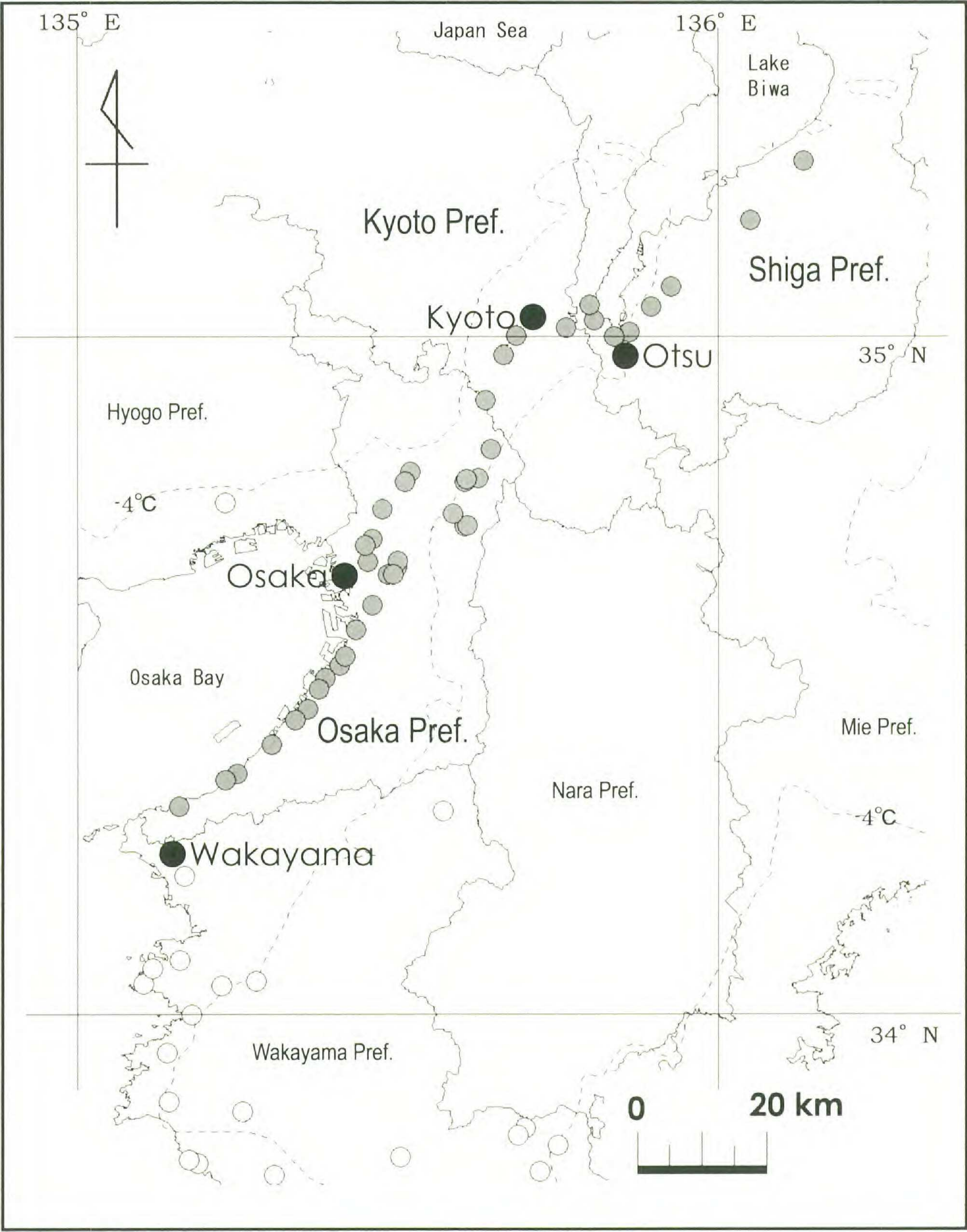


FIG. 2. Change in the distribution of *Thelypteris dentata* from 1983 to 2006. The open circles represent the distribution in 1983 (Kurata and Nakaike, 1983), and the gray circles represent the additional records of 2004–2006. The dashed line represents the -4°C isothermal line of the average minimum temperature (1990–2003) based on the data from the Japan Meteorological Agency website.

originated as spores in the potting soil of purchased plants, and the ferns may have survived due to a supply of water by humans. However, some ferns that invaded planters may have been removed if the owners did not like the invaders enough to retain them. Therefore, data from planters and gardens should not be used when rigorously evaluating habitat suitability for the downy maiden fern. Nonetheless, we have retained this information in Table 2 for the sake of completeness. Even if the absence of a fern in a planter or garden does not provide evidence of its absence in a region, the presence of a fern does provide evidence of its presence in that region.

Can heat island corridors explain expansion of the fern's distribution?.—Northward expansion of the range of the great Mormon butterfly (*Papilio memnon* L.) occurred at a rate of about 400 km over 22 years, from 1981 to 2003 (Yoshio, 2004; Yoshio and Ishii, 2004). The annual average expansion rate thus equals about 18 km. In contrast, the results of the present study indicate that the dispersal speed of the fern *Thelypteris dentata* is approximately 60 to 100 km over 20 years, for a rate of 3 to 5 km per year. Although the fern has expanded its distribution more slowly than the butterfly, this is likely because the butterfly can fly freely, whereas the fern sporophytes are sessile. Because the downy maiden fern grows in artificial urban habitats rather than in a natural environment such as that of forest-floor ferns, the city matrix may not function as a barrier to northward expansion of the distribution of this species. Our study focused on areas along railway lines, and almost all sites were in urban or suburban areas. In these areas, the city matrix is almost continuous and there are few geomorphic obstacles between the study sites. If this spatial structure represents a continuous warm corridor from Shiga to Wakayama, tropical or subtropical species that often grow in the Wakayama region may be capable of dispersal along these corridors to invade northern areas (Fig. 2). In contrast, fragmented forests surrounded by a hard-surfaced urban matrix generally prevent species of the forest interior from expanding easily, even if an urban heat island corridor connects two patches of forest. Urban weeds can expand their distribution more rapidly because the city matrix functions as a source of habitat, not as a barrier. If global warming continues, the distribution of such species will expand further and the species will become common across a wider range of urban areas.

The Crinum Line and heat islands.—In Japan, the Crinum Line and its effect on phytogeography is well known (Koshimizu, 1938; Nakanishi, 1980). This line represents a border formed by the line representing an average annual temperature of approximately 15°C and an annual lowest temperature of −3.5°C (Koshimizu, 1938), and is regarded as the standard distribution limit for subtropical or tropical species (Nakanishi, 1980). This line is still used as the distribution borderline for not only *Crinum asiaticum* L. var. *japonicum*, the species that gives the line its name, but also for various subtropical and tropical species, including *Hibiscus hamabo* Sieb. et Zucc, *Canavalia lineata* (Thunb.) DC., *Chloranthus glaber* (Thunb.) Makino, *Debregeasia edulis* (Siebold & Zucc.) Wedd. and many more (Taniguchi, 1956; Murata, 1968; Horikawa, 1976; Nakanishi, 1980). The annual average temperature and

annual lowest temperature (1983 to 2005; Table 1) at Hikone City are 14.7°C and -3.7°C, respectively, and these values approach those that define the Crinum Line. Moreover, the minimum temperatures of the Kyoto and Osaka hot spots and the heat island corridor that lies between them are higher than the minimum of -4°C (Table 1; Fig. 2), thus temperatures in this region should be capable of supporting subtropical or tropical plants. When this corridor continues to northern Shiga Prefecture, the distribution expansion of this fern may be supported further. In Kyoto City, tropical plants such as the formerly rare species *Epipogium roseum* (D. Don) Lindl. and the subtropical species *Dioscorea bulbifera* L. have been discovered (Murata, 1998). In Kyoto City, the rapid increase in the escape of the woody plant species *Litsea cubeba* in recent years was reported by Nakamura and Kobayashi (2003). The original distribution of this species is in warmer southern areas of Japan close to subtropical areas (Nakanishi, 1996). It will likely be difficult to definitively conclude whether the expanded distribution of plant species has resulted from global warming without more examples, but the present research suggests that *T. dentata* will provide one such example.

Conclusions.—We investigated the range expansion of *Thelypteris dentata* in three prefectures of Japan's Kinki District since 1983, with a focus on the possible relationship between this change and warming of the environment. There is considerable evidence that *T. dentata* is an invasive alien species, and in almost all Japanese examples, *T. dentata* has been found growing on artificial structures such as stone walls; to date, it has never migrated into forest-floor environments. Therefore, this weedy fern appears unlikely to pose a serious risk of damage to natural Japanese ecosystems.

The current study leaves room for future research to resolve gaps in our knowledge. One such gap relates to elucidation of the life history of *T. dentata*. The nature of this species should be discussed, for example, using a phenological approach to determine its responses to seasonal or temperature changes, or using comparisons with other species, to more deeply understand its adaptations to the urban environment and its high rate of distribution expansion. Second, testing the heat island corridor hypothesis will require surveys of the genetic relationships among the different populations of *T. dentata*. Third, if the distribution of *T. dentata* continues to expand, we should attempt to predict its future distribution. Although this would be difficult based solely on local-scale observations, it may become possible by means of GIS analysis.

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